# Two New Species and a Reassessment of Synonymy in the Navarretia pubescens Complex (Polemoniaceae) of Western North America 

Leigh A. Johnson<br>Department of Biology and the S. L. Welsh Herbarium, 401 WIDB, Brigham Young University, Provo, Utah 84602, U.S.A. leigh_johnson@byu.edu

Abstract. Two new species in the Navarretia pubescens (Bentham) Hooker \& Arnott complex of section Mitracarpium Brand are described: N. gowenii L. A. Johnson and N. ojaiensis Elvin, J. M. Porter \& L. A. Johnson. Navarretia gowenii is known from disjunct locations in Contra Costa and Stanislaus counties of California. Navarretia ojaiensis is known from Ventura County, California. Additionally, examination of type specimens suggests N. mitracarpa Greene, presently placed in synonymy under $N$. pubescens, be recognized as a species distinct from the latter taxon, whereas $N$. jaredii Eastwood be recognized as a synonym of $N$. mitracarpa.

Key words: IUCN Red List, Navarretia, Polemoniaceae.

Navarretia Ruiz \& Pavón sect. Mitracarpium Brand circumscribes ca. eight species that are distinguished from other Navarretia by their externally pubescent corollas, calyx ribs that are wider at the base than the intercostal membrane, and fruits that dehisce upward from the base. Section Mitracarpium is further divided into two informal species complexes: those with axes of upper leaves and often bracts expanding above the middle into a somewhat ovate rachis, and those with upper leaves and bracts that retain a narrow, linear rachis throughout the length of the organ. This feature is used as a key character by Day (1993), with only $N$. pubescens (Bentham) Hooker \& Arnott, typically with an expanded terminal leaf segment, occasionally found with only a linear upper rachis. Nuclear ribosomal ITS sequences (Spencer \& Porter, 1997) indicate these two groups are reciprocally monophyletic. Following Day (1993), this broad-axis group, hereafter referred to as the $N$. pubescens complex, comprises three species: N. pubescens, N. jaredii Eastwood, and $N$. setiloba Coville. A fourth species, $N$. mitracarpa Greene, which is encoumtered in floras prior to Day's (1993) treatment and on many herbarium sheets, was synonymized by Day under $N$. pubescens. Other names currently synonymized under the above taxa have never been widely accepted.

Recent field and herbarium work has brought to light two new species that clearly belong in Navarretia
sect. Mitracarpium. Expanded axes of the upper leaves and often bracts, deeply lobed cotyledons, and DNA sequences from the nuclear ITS and noncoding chloroplast regions (Johnson, unpublished) further ally these putative species with the $N$. pubescens complex. Here, a key to the N. pubescens complex is presented that reflects the nomenclatural changes proposed herein. Two new species, N. gowenii L. A. Johnson and N. ojaiensis Elvin, J. M. Porter \& L. A. Johnson, are proposed. Synonymy of names within the $N$. pubescens group is re-evaluated against type material, with adjustments to current synonymy suggested. All work was completed under the framework of the unified species concept (de Queiroz, 2005) using consistent character differences as an operational method for species delimitation (Snow et al., 2003; Sites \& Marshall, 2004).

Keit to Species of the Navarretta pi begecis Comples
la. Plants $\pm$ taller than broad with a dominant, erect central axis; secondary branches shorter than, and lypically not exceeding, the primary axis in absolute length or the terminal inflorescence of the primary stem in overall height.
2a. Inner bract axis usually expanded below and above the middle; upper stem, bracts, and calyces minutely puberulen, with elongate trichomes, if present, restricted to a narrow band around the midsection of the calyx or the upper portion of the bract base. . . . . N. setiloba
2 b . Inner bract axis usually expanded only below the middle; upper stem, bracts, and calyces puberulent to short-glandular, with elongate trichomes common and conspicuous on bracts and calyces . . . . . . . . . . . . . . . . . . . . . . . . 3a. Corolla lobes, throat, and tube bluepurple; anthers exserted to corolla lips or beyond; stigma exserted . . . .N. pubescens 3b. Corolla lobes and tube white to cream with a purple spot at the anastomoses of the corolla veins (veins below the anastomoses also drying purple): anthers included to exserted below middle of corolla lobe; stigma included. . . . N. gowenii
1b. Plants $\pm$ as broad as tall, branching from near the base, secondary branches often equaling or exceeding the primary axis in absolute length and the terminal inflorescence of the primary stem in overall height

† ıəqunn ' LI ə əunjo^
eous and linear abaxially, connecting at the base; htercostal membrane $V$-shaped, narrower a glandular externally to base, internally only on free portion of the lobes, the glands short-stipitate near calyx base and becoming longer near mouth of calyx 2 mm ; lobes, throat, and tube white (drying cream) with purple dots at base of corolla lobes and purple streaking (along vasculature) in throat; stipitate-


 obes; anthers ca. 0.9 mm , pollen white, spheroidal, pantoporate with sexine semitectate, reticulate, and heterobrochate; ovary situated on a nectary disk; style each lobe ca. 0.4 mm . Capsules ca. 3.8 mm , with an







Distribution and IUCN Red List category. Navarretia gowenll is known from three sites no more than
1 km apart in the Lime Ridge Open Space in Contra Costa County, California, and a third population represented by a single collection 110 km southeast made on serpentine soils on private land in Stanislaus
County. This latter material has slightly longer County. This latter material has slightly longer
stamens, with anthers extending beyond the orifice







 anknown; however, what is known about its distribution and population size suggests the plant is
vulnerable and further study is warranted.
 Gowen, an avid naturalist, plant enthusiast, and





Figure 1. Navarretia gowenii L. A. Johnson. - A. Photograph of unmounted specimens from the type collection (Gowen 390 ). -B. (inset) Illustration of opened corolla with style, following post-pollination dehiscence and showing relative position of stamens and vasculature in corolla lobes and hase (Gowen 102, BRY).
contributions to this author's study of Navarretia. Mr. Gowen's consideration of detail, love of nature and fieldwork, and persistence are admirable traits worth emulation by all students of botany.

Discussion. The included style and included to barely exserted stamens set Navarretia gowenii apart from all other members of the $N$. pubescens group. Though it shares similar corolla coloration with $N$.

Johnson<br>Navarretia pubescens Complex (Polemoniaceae)

2007
ojaiensis, it differs from this species in a number of characters detailed in the discussion of this latter taxon.

Paratypes. U.S.A. California: Contra Costa Co., Lime Ridge Open Space, NW end, ca. 600 ft., 13 June 2004, D. Gowen 102 (BRY, JEPS); Lime Ridge Open Space, summit area just S of antenna facility, 11 May 2004, D. Gowen 59 (JEPS); Stanislaus Co., Quinto Canyon at Bald Eagle Mine, T8S R7E SE1/4 of SW1/4 S32, canyon bottom setting on serpentine, 26 May 1995, D. W. Taylor 14923 (JEPS [2]).
2. Navarretia mitracarpa Greene, Pittonia 1: 135. 1887. Gilia mitracarpa (Greene) Rattan, West Coast Botany 53. 1898. TYPE: U.S.A. California: Lake Co., June 1884, K. Curran s.n. (holotype, NDG digital image seen; isolypes, CAS, GH not seen, NY digital image seen, UC, US).

Navarretia jaredii Eastwood, Zoe 5: 89-90. 1900. Gilia jaredii (Eastwood) K. Schumann, Just's Bot. Jahresber. 28: 489. 1902. Navarretia mitracarpa Greene subsp. jaredii (Eastwood) H. Mason, III. Fl. Pacific States 3: 448. 1951. TYPE: U.S.A. California: San Luis Obispo Co., Paso Robles Creek, May 1897, L. Jared s.n. (holotype, CAS).
Navarretia mitracarpa Greene var. villosa Hoover, Vasc. Pl. San Luis Obispo Co., Calif. 229. 1970. TYPE: U.S.A. California: San Luis Obispo Co., betw. Rocky Butte \& Pine Mtn., Santa Lucia Range, 21 June 1950, R. Hoover 8006 (holotype, OBI).

Navarretia mitracarpa was generally accepted as a distinct taxon in floristic treatments prior to Day (1993). Day considered N. mitracarpa conspecific with $N$. pubescens, but did not elaborate her rationale, a position apparently also accepted by Spencer (Spencer \& Porter, 1997) based on his annotation of the isotype specimen at US. Type material of $N$. mitracarpa differs from $N$. pubescens in its spreading rather than upright habit, and, as evident on the material at US, the corolla throat is white rather than bluish purple. Brand (1907) recorded four deeply divided cotyledons in this species; this is likely a typographical error, and instead he meant two deeply divided cotyledons that appear as four linear segments. Jepson (1943) records (from V. L. Bailey's dissection of the UC isotype) "...cotyledons as if 6 , each of the two cotyledons deeply parted into 3 lobes" and S. C. Spencer, in the fragment pack on the isotype specimen at US, records just four segments (with the embryo still available for observation). My own survey from multiple populations and multiple stages of development of taxa in this complex shows that the number of cotyledons can vary from two to three within a single population of $N$. gowenii, $N$. pubescens, and $N$. mitracarpa, and that individual cotyledons are invariably deeply 2 -lobed so as to appear as if
cotyledons are four or six in number ( $N$. setiloba and N. ojaiensis showed only three cotyledons, but only two seeds from a single population each were available for study). Such variation within populations diminishes the taxonomic value of cotyledon number for distinguishing among taxa in this group.

The placement of Navarretia mitracarpa under synonymy of $N$. pubescens at first seems plausible because the type locality of $N$. mitracarpa is listed as Lake County, California, and the only other presently known member of the $N$. pubescens group in Lake County is $N$. pubescens. However, Jepson (1943) noted that K. Curran's collecting habits were disorderly; although she may have been in Lake County in June 1884, this does not exclude the possibility of other collections elsewhere that month, or that the date itself is correct. Indeed, the holotype records the date as August 1884, the specimen at UC lists June, and the specimens at NY and US have no date at all, but are labeled "part of the type." The fact that Curran (Brandegee, 1893) herself considered N. mitracarpa to be conspecific with N. filicaulis (Torrey ex A. Gray) Greene (as Gilia filicaulis Torrey ex A. Gray) suggests that she considered it distinct from N. pubescens even if she was not correct in her assessment of its affinities. In deference to the characters observable on the types, this author considers $N$. mitracarpa distinct from $N$. pubescens, but indistinct from $N$. jaredii.

Material presently identifiable to Navarretia jaredii, following Day (1993), is here referred back to $N$. mitracarpa. Mason (1951), who treated N. jaredii as a subspecies of $N$. mitracarpa, indicated the former has a larger flowering head than the latter. However, as noted by Hoover (1970), the type sheet for $N$. jaredii has four specimens on it, and the original description describes the upper two, smaller-headed plants, not the lower two, larger-headed individuals. The smallheaded individuals are consistent in characteristics, insofar as development can ascertain, with both the types and original descriptions of $N$. mitracarpa. Hoover (1970: 229) suggested the lower two plants, which are developmentally immature and lacking flowers, may be $N$. pubescens; whether this is the case or they simply represent ecological plasticity cannot be presently determined. This author follows Hoover in placing $N$. jaredii as a synonym of $N$. mitracarpa. Hoover (1970: 229) further distinguished a typical variety mitracarpa and a more densely pubescent form, N. mitracarpa var. villosa. There is noticeable variation in pubescence among collections of this species, but the geographic integrity of such variation and its correlation with other observable features has yet to be fully ascertained. The spreading habit of $N$. mitracarpa may be ecologically plastic: the larger-headed individuals from the type sheet for $N$. jaredii are upright rather
than spreading in habit, and similar upright forms with larger heads that are clearly allied with $N$. mitracarpa rather than $N$. pubescens in floral features have been collected in tall grass by this author. These are not distinguishable from typical $N$. mitracarpa by a suite of rapidly evolving, noncoding chloroplast regions (Johnson, unpublished).
3. Navarretia ojaiensis Elvin, J. M. Porter \& L. A. Johnson, sp. nov. TYPE: U.S.A. California: Ventura Co., Ventura River Basin, meadow betw. Calif. Prep. School \& Ojai, 15 June 1948, H. M. Pollard s.n. (holotype, UC1008707; isotypes, RSA43448, SBBG98249). Figure 2.

Species nova ab Navarretia mitracarpa Greene lobis corollae albis (non azureis), acuminato-cuspidatis (non rotundatis) differt.

Taprooted annuals; low and spreading to more often erect, primary axis $4.2-32.5 \mathrm{~cm}$ tall; stems hirsute to glandular-pilose, 0.9-2 mm diam., tawny yellow, pale green suffused with purple, to strongly anthocyanic; frequently branching from the base, the lowest branches 4.4-18.2 cm. Leaves 12-32 mm, bipinnately dissected, bright green, glandular-pilose; lateral lobes $3.5-7.5 \mathrm{~mm}$, narrow and often acerose; terminal lobe $12-18 \times 1.5-4 \mathrm{~mm}$, narrowly rhombic to narrowly obtrullate, dentate-aculeate, the teeth to 3 mm ; leaves only slightly reduced in size on distal stems. Inflorescences glandular-pilose, terminating primary and secondary (and occasionally third order) branches, capitate, bracteose, bracts pungent; flowers in cymose dichasia; head $8-32 \mathrm{~mm}$ diam.; inflorescence bracts like the upper cauline leaves, $10-17 \mathrm{~mm}$, bipinnately dissected, glandular-pilose; lateral lobes $1-4.5 \mathrm{~mm}$, usually acerose; terminal lobe $7-13 \times 0.5-2 \mathrm{~mm}$, linear to narrowly rhombic, dentate-aculeate. Floral bracts 6-10 mm , pinnately dissected, glandular-pilose; with (1) 2 to 3 lateral lobes, lobes narrow, acute to acerose; terminal lobe $2.5-3.5 \mathrm{~mm}$, linear, acerose; calyx campanulate to tubular, $6.5-9.6 \mathrm{~mm}$, glandularpilose; lobes unequal in length and usually polymorphic, 3-6.5 mm, linear and entire to pinnatifid with 3 to 5 acute to acerose lobes; calyx tube short, 23.3 mm ; the green costae of lohes much broader than hyaline portion of calyx tube, sinuses V -shaped; corolla funnelform, $5.9-10.3 \mathrm{~mm}$; tube $3-5.8 \mathrm{~mm}$, white, glandular-pilose externally, sparsely hairy internally on distal tube; throat $1.5-2.6 \mathrm{~mm}$, flaring, yellowish green to whitish green, glandular-pilose on external throat, glabrous internally, lobe $1.4-2.2 \mathrm{~mm} \times 0.9-$ 1.3 mm , lanceolate, acute and somewhat cuspidate, sparsely glandular-puberulent on abaxial surface, white with a violet patch along vasculature at juncture of proximal lobe and distal throat; stamens epipetalous,
filaments diverging from corolla subequally, free portion subequal in length, $2.2-3.9 \mathrm{~mm}$, sparsely hairy proximally, otherwise glabrous; anther $0.7-1 \mathrm{~mm}$; pollen spheroidal, variable in size. 35.2$54.3 \mu \mathrm{~m}$ diam.; pantocolporate, apertures 22 to 28 , ora circular, $3-5.2 \mu \mathrm{~m}$ in diam., sexine overlapping ora with irregularly angular colpi, 2.5-4.4 $\mu \mathrm{m}$ in diam.; exine ca. $2.5 \mu \mathrm{~m}$ thick; microreticulate, heterobrochate, the lumina $0.2-1 \mathrm{~mm}$ diam.; pollen creamcolored; ovary $0.9-1.9 \mathrm{~mm}$ tall, $0.4-0.7 \mathrm{~mm}$ broad, obovoidal, with a thickened stylar base, glabrous; style $5.4-8 \mathrm{~mm}$, glabrous; sligma lobes $2,0.3-0.4 \mathrm{~mm}$, spreading when receptive; ovules one per locule, only one maturing and the locules not remaining distinct; nectary disk forming a 5 -lobed collar at ovary base, $0.4-0.6 \mathrm{~mm}$ diam., rising 0.3 mm along the ovary, and $0.1-0.2 \mathrm{~mm}$ deep, pale green in color. Fruit $2.2-$ 3.2 mm tall, $0.8-1.1 \mathrm{~mm}$ diam., straw yellow, capsule dehiscing loculicidally and septicidally from base, obovoidal, apiculate, apicule $0.3-0.7 \mathrm{~mm}$; seed solitary, $2-3 \mathrm{~mm}$ long, $0.5-0.9 \mathrm{~mm}$ broad, narrowly obovoidal, golden to tan in color, seed surface smooth, anticlinal walls of seed coat only weakly visible, seed surface ornamentation not evident at $1000 \times$ or $10,000 \times$; seed coat becoming mucilaginous when wetted, the outer periclinal walls separating, sometimes in large patches, each cell of the seed coat bearing a single, massive, helical spiricle; cotyledons 3 , each deeply 2 -lobed.
Distribution and IUCN Red List category. Navarretia ojaiensis is presently known from dry, clay soils of native perennial grasslands in openings of chaparral in the Ojai Valley, Santa Clarita Valley, and Santa Susana Mountains of Ventura County, California. Proximity of the latter locations and an unverified report from the Santa Monica Mountains suggest it occurs in Los Angeles County as well. A preliminary conservation assessment places this taxon in Red List Category DD (Data Deficient; IUCN, 2001) because long-term trends are unknown and surveys are needed to identify extant populations from throughout its distribution. At least some historically known populations from Ojai Valley have likely been consumed by development, and all but one of the recently identified populations from the Santa Clarita Valley and adjacent Santa Susana Mountains are likewise threatened by development; one population from this latter region lies in an area to be "conserved," but all sites in this region continue to be threatened by grazing.

Etymology. The specific epithet, literally "from Ojai," refers to the Ojai Valley of Ventura County, California, where many early collections of the species were made over a period of 30 years by Henry Pollard.


Figure 2. Navarretia ojaiensis Elvin, J. M. Porter \& L. A. Johnson. - A. Photograph of holotype specimen (Pollard s.n., UC). -B. (inset) Illustration of opened corolla with style, following post-pollination dehiscence and showing relative position of stamens and vasculature in corolla lobes and base (Elvin 2930, BRY).

Discussion. Navarretia ojaiensis is clearly similar to $N$. mitracarpa in its spreading habit but differs consistently in flower coloration and in the acuminate corolla lobes. Navarretia ojaiensis is similar to $N$.
gowenii in flower coloration but differs in its spreading rather than primarily upright habit, its acuminate-cuspidate corolla lobes (rather than round-ed-acute), long exserted stamens and exserted style,
a longer apical nipple on the fruit, in the proportionally shorter fusion of the calyx segments, and in the distance from the base that the three primary corolla lobe veins gradually diverge (greater than 1 mm ), rather than the relatively abrupt divergence at or near (less than 0.5 mm ) the base in N. gowenii.

Paratypes. U.S.A. California: Ventura Co., Foothills Trail, ca. 0.5 mi . W of Gridley Canyon Rd., Ojai Valley, 4 June 1970, Henry M. Pollard s.n. (RSA468364. SBBG39322); Hermosa Rd. near San Antonio Creek bridge at Camp Comfort, Ojai Valley, 9 June 1970, H. M. Pollard s.n. (CAS540889, RSA468363, SBBG40084): Foothills Trail. Ojai Valley, 8 May 1960, H. M. Pollard s.n. (CAS479004, SBBC37480); Santa Clarita Valley, hills N of SR 126, just W of Ventura/Los Angeles Co. line, Newhall Ranch, 9 June 2003, M. A. Elvin 2930 (BRY, RSA); Santa Susana Mtns., N side of range in Salt Canyon watershed, Newhall Ranch, 12 June 2003, M. A. Elvin 2941 (BRY, MO); Santa Susana Mtns., N side of range in Salt Canyon watershed, Newhall Ranch, 1 July 2003, M. A. Elvin 2963 (BRY, RSA).
4. Navarretia pubescens (Bentham) Hooker \& Arnott, Bot. Beechy Voy. 368. 1839. Basionym: Aegochloa pubescens Bentham. Bot. Reg. 19: under pl. 1622. 1833. Gilia pubescens (Bentham) Steudel, Nomencl. Bot., ed. 2 (Steudel) i: 684. 1840. TYPE: U.S.A. California: D. Douglas 1833 (holotype, K digital image seen).

Navarretia erecta A. Heller, Muhlenbergia 1: 146. 1906. TYPE: U.S.A. California: Mendocino Co.. near Ukiah, 11 July 1902, A. A. Heller s.n. (holotype, BKL not seen: isolypes, CAS, GH not seen, US, NY digital image seen).

Discussion. Navarretia pubescens is one of the earliest named species in this genus established in 1794, and it has the broadest distribution among species of the $N$. pubescens complex. The habit of this species is invariably erect, with plants either possessing a single axis or producing secondary, erect axes along the primary stem. A population from Contra Costa County, California, with white corolla lobes and tube is known (Gowen 100, BRY, JEPS), but this population has a purple throat (not simply with purple spots), long exserted stamens, and copious pubescence. In contrast, the other species in this complex have a white to cream throat and tube, with purple only present on the lobes, as a spot at the base of each petal associated with the veins, or both. The erect habit and colored throat of $N$. pubescens throughout its range contrast with the habit and corolla coloration of N. mitracarpa (see above), and these features are here used to exclude this later taxon from N. pubescens.
5. Navarretia setiloba Coville, Contr. U.S. Natl. Herb. 4: 153. 1893. TYPE: U.S.A. California:

Kern Co., Kern River Valley, 900-1450 m, 23 June 1891, F. V. Coville \& F. Funston 1049 (holotype, US; isotype, UC).

Discussion. Navarrelia setiloba circumscribes material possessing inner bracts with an expanded apical axis and only puberulent hairs on the stems, leaves, bracts, and calyces (a narrow band of longer trichomes is sometimes present on the bracts and calyces as indicated in the key above). This species is primarily localized to Kern County, California, where two morphotypes exist. A broad sample of individuals and populations of each morphotype is yet needed to determine the taxonomic significance of this variation. A collection initially determined as " $N$. jaredii" from Los Angeles County (Porter 10913, RSA) is morphologically congruent with, and indistinguishable in chloroplast DNA sequence from, the blue corolla-lobed form from Kern County. Additionally, some historical collections in Kern County have been annotated by A. Day as intermediate with $N$. pubescens (e.g., JEPS 41309) and merit further study.

Acknowledgments. I thank David Gowen for his observations, for providing material of many Navarretia species to the author for study, and for help with the preliminary IUCN assessment of $N$. gowenii; Mark Elvin for contributing specimens of $N$. ojaiensis for study and for help with the technical description and preliminary IUCN assessment for this species; J. Mark Porter for observations and help with the technical description of N. ojaiensis: Libing Zhang for translating the diagnoses to Latin; Arnold Tiehm for insights on the typification of A. Heller collections; Dieter Wilken and Victoria C. Hollowell for critical review; staff at NDG, OBI, RSA/POM, SBBG, UC/ JEPS, UCR, and US for access to their collections; and the stalf at UVSC for use of their imaging equipment (supported by National Science Foundation [NSF] grant DBI-0447301 to Jim Harris). This work was supported by NSF grant DEB-0344837.

Literature Cited
Brand, A. 1907. Navarretia. Pp. 151-168 in A. Engler (editor), Das Pflanzenreich IV(250). W. Engelmann, Leipzig.
Brandegee, K. 1893. The botanical writings of Edward L. Greene. Zoe 4: 63-103.
Day, A. C. 1993. Navarretia. Pp. 844-849 in J. C. Hickman (editor), The Jepson Manual, Higher Plants of Califormia. Univ. California Press, Berkeley.
de Queiroz, K. 2005. A unified concept of species and its consequences for the future of taxonomy. Proc. Calif. Acad. Sci. 56(Suppl. 1): 196-215.
Hoover, R. F. 1970. The Vascular Plants of San Luis Obispo County, California. Univ. California Press, Los Angeles.

IUCN. 2001. IUCN Red List Categories and Criteria, Version 3.1. Prepared by the IUCN Species Survival Commission, Gland, Switzerland, and Cambridge, United Kingdom.
Jepson, W. L. 1943. A Flora of California, Vol. 3, Pt. 2. Univ. California Press, Berkeley.
Mason, H. L. 1951. Polemoniaceae. Pp. 396-474 in L. Abrams (editor), Illustrated Flora of the Pacific States, Vol. 3. Stanford Univ. Press, Stanford.

Sites, J. W. \& J. C. Marshall. 2004. Operational criteria for delimiting species. Annual Rev. Ecol. Evol. Syst. 35: 199-227.
Snow, N., G. P. Guymer \& G. Sawvel. 2003. Systematics of Austromyrtus, Lenwebbia, and the Australian species of Gossia (Myrtaceae). Syst. Bot. Monogr. 65: 1-95.
Spencer, S. C. \& J. M. Porter. 1997. Evolutionary diversification and adaptation to novel environments in Navarretia (Polemoniaceae). Syst. Bot. 22: 649-668.

